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Climate and Mountain Pine Beetle-Induced Tree
Mortality in the Selway-Bitterroot Wilderness Area

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Figure 1. "Ghost forest" of whitebark pine snags killed by mountain pine beetle during the late 1920s-1930s outbreak near Beaver Lake, Idaho in the Selway-Bitterroot Wilderness Area (Photo by K.F. Kipfmueller, 1998).

Abstract

Dendrochronological methods are used to date past beetle-induced whitebark pine mortality in three watersheds of the Selway-Bitterroot Wilderness Area, Idaho and Montana. Death dates were determined for 84 of 110 (76%) sampled whitebark pines. Whitebark pine mortality due to mountain pine beetle epidemics is clustered around a few short time periods, with the largest peak centered around 1930, a period of widespread beetle-induced mortality documented elsewhere. Mortality events also occurred in 1960s, and 1980s but are limited two only 2 watersheds. The cessation of the 1930s outbreak may be related to prolonged cold temperatures during the winter of 1930.

Aerial survey data (1966-1999) for mountain pine beetles was obtained to develop regression models to predict beetle-induced tree mortality. Two region-wide mountain pine beetle outbreaks have occurred since about 1966. The first outbreak began gradually around the late 1970s and peaked during the mid 1980s. A second epidemic started around 1994 but has not peaked. Pearson correlations between the beetle mortality data indicate the strongest relationship between beetle-induced tree mortality (total area killed) and climate relates to July precipitation ($P \leq 0.001$). Variance explained in four species-specific regression models is between 22-24%. A fifth model that incorporates past beetle mortality explains 75% of the variance.

Whitebark pine mortality due to mountain pine beetles may be relatively infrequent occurring only during periods when beetle populations are at epidemic proportions at lower elevations, or only when drought is prolonged. Rising global temperatures may increase the risk of whitebark pine habitats to more severe or prolonged mountain pine beetle epidemics by creating an environment more conducive to the life history of the beetle.

Introduction

Natural disturbances are an integral component of forested ecosystems. Disturbances have various effects ranging from total stand replacement and reinitiation of forest development, such as in high intensity crown fires, to species or age-specific mortality. Disturbances are usually characterized by their spatial extent, intensity, return interval, severity, and predictability (Pickett and White 1985). Natural disturbances create heterogeneity within forested landscapes by partitioning the landscape into patches with different environmental and ecological conditions and a shifting-mosaic (Sousa 1984; Pickett and White 1985). Temporally, disturbances may create patches asynchronously across the landscape resulting in neighboring patches of different ages (Sousa 1984). Disturbances alter nutrient dynamics, habitat structure, and diversity at both local and landscape scales (e.g., Heinselman 1981; Boerner 1982; Pickett and White 1985). Prior to widespread human impacts on forest resources, natural disturbances such as fire, windthrow, insects, and pathogens maintained western forest ecosystems in various stages of successional development.

Although fire is largely thought to be the primary disturbance that alters forest structure and composition in western coniferous forests, insect outbreaks can also have important impacts on these attributes. In some forests insects may be as important a disturbance agent as fire, and may be an integral part of maintaining forest ecosystem characteristics (Romme et al. 1986; Baker and Veblen 1990). Periodic epidemics of defoliating or phloem feeding insects can result in widespread tree mortality and initiate or enhance understory regeneration by increasing light and/or nutrient availability (Romme et al. 1986; Hadley and Veblen 1993; Veblen et al. 1994; Stone and Wolfe 1996). There may be synergistic effects between insect epidemics and other disturbances as well. For example, fallen trees killed by mountain pine beetle or needle litter may fuel widespread or intense fires (Lotan et al. 1985; Knight 1987).

During most years, populations of forest insects are small and localized, damaging only a few trees over a limited area (Nothnagle and Schultz 1987). However, predisposing factors such as changes in host food quality or defensive mechanisms, environmental conditions, or physiological changes can lead to dramatic population increases over large areas, with important implications for forests (Berryman 1987).

While population dynamics (Turchin 1990; Turchin et al. 1991; Logan et al. 1998), depredation (Rust 1930; Cole and Amman 1980), and host quality and abundance clearly play an important role in the onset and duration of insect epidemics, the role of climate in regulating periodic outbreaks of forest insect populations is not well understood. Climate influences insect population numbers, and can affect the physiological capacity of trees to resist attack (Martinat 1987; Waring and Cobb 1992; Swetnam and Lynch 1993; Hunter and Price 1998). Temperature has a direct effect on insects by regulating biological cycles such as reproduction and emergence behavior e.g., (Cole 1981; Logan et al. 1998), and inducing mortality during abnormally warm or cold periods (Cole and Amman 1980). Michaels (1984) found mild winter temperatures were associated with southern pine beetle outbreaks that may have been related to decreased mortality of over wintering broods. Cool conditions may also directly affect insect population dynamics. Cold temperatures, for example, can result in significant mortality in over wintering broods of bark beetles, or limit the dispersal and colonization effectiveness of some insect pests (Evenden 1936; Amman and Cole 1983; Safranyik 1989).

The indirect effects of climate on insects include reductions in host capacity to resist insect attacks or changes in the food quality of host species. Water-induced stress, for example, may limit host capacity to produce defensive compounds such as oleoresin that inhibit successful attack (Coulson 1979). Ferrell (1996) showed that increased tree mortality in the Sierra Nevada during the late 1980s coincided with extreme drought conditions, followed by localized bark beetle attack on drought-weakened trees. In lodgepole pine forests, Thomson and Shrimpton (1984) determined that warm and dry conditions toward the end of the growing season were favorable for mountain pine beetle populations and may have caused a reduction in tree resistance to beetle attack. Wetter than normal conditions have also been associated with outbreaks of foliage feeding insects such as the western spruce budworm (*Choristoneura occidentalis* Freeman)(Mattson and Haack 1987; Swetnam and Lynch 1993; Swetnam and Betancourt 1998; Ryerson 1999). Favorable climate conditions for tree-growth may result in reduced cuticle production and larger plant tissues in some host species providing a more suitable food source for phytophagous insects (Larsson 1989).

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is an economically and ecologically important forest insect of western coniferous forests. The principal hosts of mountain pine beetle include ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), and whitebark pine (*Pinus albicaulis*). Completing their life cycle under the bark of host trees, beetles construct egg galleries and larvae feed on the infected tree's inner phloem (Amman et al. 1989). Gallery construction can lead to girdling of the tree impeding water and nutrient transport within the tree. In addition, mountain pine beetles carry a secondary pathogen, a blue staining fungus, that clogs the sapwood of living trees preventing the transport of water and nutrients within the tree (Amman et al. 1989). It is this secondary pathogen that is often responsible for tree mortality (Amman et al. 1989). Outbreaks of mountain pine beetle can last 3-20 years and result in region-wide mortality of host species, usually concentrated within trees in the larger size classes (Safranyik 1989). An epidemic of mountain pine beetle occurring between about 1924 and 1934 killed large areas of lodgepole and whitebark pine in northern Rocky Mountains (Evenden 1944). During 1932, the peak of the mountain pine beetle outbreak in the Beaverhead National Forest, more than 17 million trees were killed by the beetle (Evenden 1934).

Although numerous tree species are affected by mountain pine beetles, whitebark pine (*Pinus albicaulis* Engelm) may be at the greatest ecological risk. Whitebark pine is a keystone species of subalpine forest ecosystems, providing watershed protection, aesthetics, habitat, and food for wildlife, such as the Clark's nutcracker and black and grizzly bears (Arno and Hoff 1990). Due to an introduced pathogen, changes in fire regimes, and advancing succession, whitebark pine has declined dramatically across half of its range (Keane and Arno 1993, Kendall and Keane, 2001, Tomback et al. 2001). Whitebark pine populations have declined by as much as 42% in the past 20 years in parts of the northern Rocky Mountains (Keane and Arno 1993). The area dominated by whitebark pine has declined by more than 45% in the US portion of the Interior Columbia Basin (Keane 2001). On sites where it is seral to other conifers, whitebark pine has declined more than 98% (Keane et al. 1996). Twentieth-century die-offs of whitebark pine are evident today as "ghost forests" of standing dead trees in broad swaths across the highest elevations in Idaho and

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Montana (Figure 1) (Ciesla and Furniss 1975). Many trees were killed by white pine blister rust (*Cronartium ribicola*) (Lachmund 1926; Hoff and Hagle 1990, McDonald and Hoff 2001) and mountain pine beetle (Bartos and Gibson 1990). The blister rust is a Eurasian fungus that was introduced to the Pacific Northwest in 1910 (Hoff and Hagle 1990), whereas the mountain pine beetle is a native forest insect. Although it is known that these two agents were proximate causes of much of the whitebark pine mortality that occurred during the 20th century, drought and fire suppression may have predisposed whitebark pine to mortality.

Climatic factors such as temperature variability are thought to play an important role in regulating populations of mountain pine beetle (Amman and Cole 1983). Mild winter temperatures promote survivorship of over wintering mountain pine beetles while anomalous cold events lead to increased brood mortality within infected trees (Evenden 1936; Amman and Cole 1983). Mild summer temperatures also appear conducive to mountain pine beetle survivorship, while extreme warm events can lead to increased brood mortality and decreased beetle activity.

While temperatures have important direct effects on mountain pine beetles, temperature and precipitation regimes affect host species such as lodgepole and whitebark pine and can have a cascading effect on beetle epidemics. Moisture stress is widely regarded as an important agent that predisposes conifers to mortality by colonizing bark beetles (Craighead 1925; Thomson and Shrimpton 1984; Safranyik 1989). Host species experience moisture stress induced by a combination of warm temperatures and limited rainfall during the summer throughout most of the beetles range. Extreme moisture stress often results in reduced resin flow, limiting the host's capacity to resist attack. At moderate stress levels however, a tree's energy stores are used in resin production rather than for radial growth, which may limit the effectiveness of beetle attacks (Lorio 1986; Lorio and Sommers 1986). Endemic populations may build slowly by overwhelming the defenses of individual, scattered trees weakened by pathogens such as dwarf mistletoe, root diseases, or lightning or other storm damage (Tkacz and Scmitz 1986; Amman and Schmitz 1988; Schowalter and Filip 1993; Nebeker et al. 1995). Trees that are growing vigorously are apparently able to repel most attacks so long as beetle populations are low and tree-growing conditions are

favorable. However, drought may create moisture stress over a broad region predisposing a large number of trees to successful beetle attacks resulting in rapid beetle population expansion to epidemic proportions (Safranyik 1989).

The role of climate in regulating outbreaks of mountain pine beetles remains elusive. Climate may impact beetle populations directly but also likely effects host trees' capacity to resist attacks. Our limited understanding of the relationships between climate variability and beetle epidemics warrants a long term perspective. An understanding of beetle-climate relationships is important in the face of evidence suggesting climate is warming, with anthropogenic activities implicated as the most likely culprit (IPPC 2001). Increasing temperatures may permit beetle populations to expand more readily into upper elevations dominated by whitebark pine, possibly leading to more frequent and severe epidemics than had occurred in the past. Knowledge of the relationship between beetles, climate, and their hosts can help develop future management strategies should climate continue to warm. Long term perspectives necessary to establish the important linkages between beetles and climate can be developed by examining tree-ring evidence of beetle-induced mortality, an important supplement to the more systematic aerial monitoring that began in the 1960's. This research examines the role of climate in beetle epidemics in the Selway-Bitterroot region of the northern Rocky Mountains (Figure 2). Our research has two main goals. First, dendrochronological techniques are used to determine the dates of past bark beetle-induced tree mortality of whitebark pine occupying upper elevations in the Selway-Bitterroot Wilderness Area. These death dates will help extend the record of beetle mortality further into the past than aerial survey methods. Climatic relationships between dendrochronologically determined dates of mountain pine beetle epidemics are assessed using graphical and statistical analysis. Secondly, aerial survey data is used from three National Forests with administrative responsibility within the Selway-Bitterroot Wilderness Area to quantitatively assess the relationship between more recent mountain pine beetle epidemics and climate. Correlation and regression techniques are used to determine the strength of the relationship between various climate variables and mountain pine beetle-induced tree mortality. Our specific hypotheses relating mountain pine beetle epidemics to climate include:

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1) Mountain pine beetle epidemics are synchronous over large (multiple National Forests) areas.

2) Region-wide outbreaks are related to drought conditions that predispose hosts to successful colonization by mountain pine beetle.

3) Unusually cold winter conditions reduce beetle-induced tree mortality during the following summer.

Study Area

The primary area of interest in this study is the Selway-Bitterroot Wilderness Area (SBW) located on the border of Idaho and Montana in the Northern Rocky Mountain Physiographic Province (Figure 2). Established in 1964 with the passage of the Wilderness Act, the SBW includes approximately 542,000 ha, representing the third largest wilderness area in the conterminous United States. The SBW is administered jointly by four National Forests of the Northern Region of the United States Forest Service: the Bitterroot, Clearwater, Lolo and Nez Perce. Adjacent to the SBW, separated by only a one-lane dirt road, is the Frank Church River of No Return Wilderness (958,177 ha), the largest wilderness area in the conterminous United States.

The SBW is topographically diverse, divided into eastern and western portions by the Bitterroot Mountains. The western portion encompasses the largest land area. More moderate slopes, lower peaks and more contiguous forest typify this portion of the wilderness. The Bitterroot Mountains form the eastern boundary of the SBW. The Bitterroot Mountains are a rugged mountain chain running generally north-south characterized by parallel (east-west trending) glaciated valleys and 3,000 m+ peaks. Elevation ranges from 463 m along the Selway River in Idaho to 3,048 m on Trapper Peak. The vegetation composition reflects the topographic complexity of the SBW. Ponderosa pine-Douglas-fir (*Pseudotsuga menziesii* Mirb.) habitats characterize lower forest zones, merging to lodgepole pine and Engelmann spruce-subalpine fir (*Picea engelmannii* Parry-*Abies lasiocarpa* (Hook.) Nutt.) with increasing elevation (Crane & Fischer 1986). Long-lived whitebark pine (*Pinus albicaulis* Engelm.) and subalpine larch (*Larix lyallii* Parl.) are found at the highest elevations and on more extreme sites (Arno and Habeck 1972).

Three watersheds were selected for dendrochronological dating of mountain pine beetle mortality (Figure 2, Table 1). These watersheds are separated by 55-125 km and are between 2,000-2,500 m elevation (Figure 2). The watersheds are cirque basins, with steep headwalls and gradually sloping valley floors. Forest composition is variable consisting of large patches of lodgepole pine of around 100 years in age with older forests composed of spruce and fir interspersed throughout. Stands of whitebark pine (mostly dead standing snags) are located on ridges surrounding the basins. These stands have variable amounts of regeneration, mostly composed of subalpine fir and Engelmann spruce. The Baker Lake watershed also has a significant subalpine larch component.

Methods

Dendrochronological Methods

Increment cores were collected from whitebark pine snags exhibiting characteristic "J" shaped galleries typically diagnostic of mountain pine beetles (Wood 1982; Amman et al. 1989). Two or more increment cores were collected from each tree to increase the potential for collecting the outer ring and to facilitate crossdating. Increment cores were stored in paper drinking straws for transport back to the laboratory. In addition, partial cross sections (Arno and Sneck 1977) were removed from fire-scarred trees that had been subsequently killed by mountain pine beetles. Fire-scarred trees were collected in each watershed as part of an ongoing fire history study (Kipfmueller in prep.). The degree of weathering, presence of blue-stain on samples, presence of "J" shaped galleries, and diameter at breast height were recorded for each sampled tree.

Increment cores and cross-sections were crossdated following standard dendrochronological dating techniques (Stokes and Smiley 1968). Samples that could not be dated using standard skeleton plotting techniques were measured to the nearest 0.01 mm and growth patterns were compared to master dating series developed for a climate reconstruction study in the region using program COFECHA (Holmes 1983). Possible tree-ring dates suggested by COFECHA were verified by reexamining the sample visually to ensure accuracy. Probable death dates were assigned by examining

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the outer ring formed for the presence of latewood, making a determination based on the degree of weathering, field notes indicating the presence of beetle galleries, and increment core quality. Paired cores were also compared to ensure a correct outer date was identified. The latest date was used as the death date on paired increment cores with outer rings one or two years different but that otherwise appeared to be of good quality. Death-dates from the three watersheds were pooled to provide a regional perspective on beetle mortality through time and to provide a larger sample size than would be available if only individual watersheds were examined. Graphical comparisons were made between the dendrochronologically derived death dates and climate variables to assess the potential association between beetle mortality and climate variables.

Aerial Survey Data

Estimates of area of forest killed by mountain pine beetle between 1960-1999 was obtained from the United States Forest Office of the Northern Region in Missoula, MT. These data were collected using aerial flight surveys to detect mortality due to insects and other pests (McConnell et al. 2000). Data for three National Forests that administer lands in the Selway-Bitterroot Wilderness Area (Bitterroot, Lolo, and Nez Perce National Forests) were used for analyses. Data for the Clearwater National Forest, also administering portions of the SBW, were omitted due to limited data (data available only for 1986-1998). Data is mostly complete for the three remaining forests between 1967-1999. Aerial survey data records the area impacted by mountain pine beetle and other insect pests the year following the mortality. For example, acreage recorded during surveys conducted during 1999 reflects beetle mortality that occurred during 1998 (Ken Gibson, Pers. Comm.). Therefore, the aerial survey data covers the time period from 1966-1998. Aerial surveys record areas of tree mortality delineated by the principal species killed (e.g., ponderosa, lodgepole, and whitebark pine) and attributed to mountain pine beetle or other agents.

Total hectares killed by mountain pine beetles was plotted for the three National Forests separately to examine the spatio-temporal patterns of beetle mortality and assess the regional synchrony of mountain pine beetle epidemics. These time series

were based on the percentage of the forest killed by mountain pine beetle in each National Forest calculated by dividing the area killed by the total hectares included within individual National Forest boundaries. A regional time series of the percentage of National Forest area affected by mountain pine beetle was constructed by summing the area affected and calculating the percentage of the area as a whole for each year. This includes extensive areas outside the wilderness area but provides an important regional perspective. Forests lacking a record of mountain pine beetle activity were omitted from the analysis during some years. For example, data is missing for the Nez Perce National Forest during 1972, so the percentage of the area affected by mountain pine beetle was calculated by omitting the area included in the Nez Perce National Forest during that year.

Aerial survey data are somewhat incomplete in that mortality is often attributed to a specific cause (e.g. mountain pine beetle) but not verified on the ground. It is possible that some of the mortality observed in these forests is due to other agents but has been erroneously assigned to the mountain pine beetle. Blister rust mortality could possibly be misconstrued as beetle-induced mortality because the extent was not assessed. However, whitebark pine that have been infected with blister rust may be more susceptible to successful mountain pine beetle attack (Keane et al. 1994) and therefore mortality identified as beetle-induced may actually represent the interaction between the two disturbances.

Climate-Beetle Interactions

Climate-beetle relationships were examined using graphical techniques as well as Pearson correlations and regression models. We examined the influence of climate on beetle-induced tree mortality using the total hectares killed for the three National Forests encompassing the SBW as well as hectares affected in lodgepole pine and whitebark pine host forests. Aerial survey data was square root transformed for the statistical analyses in order to more closely approximate a normal distribution.

Climate data for comparison with beetle-induced tree mortality was obtained from the National Climatic Data Center. Average monthly temperature, total monthly precipitation, and average monthly Palmer Drought Severity Index (PDSI) data from

1900-2000 for Idaho Climate Division 4 (Central Mountains) were obtained to examine the relationships between climate variability and mountain pine beetle activity. Idaho Division 4 data were selected because it includes the majority of the area encompassed by the aerial surveys and most of the area within the wilderness. We used temperature data for winter months (December-March) and summer months (June-August), summer precipitation (June-August) and Palmer Drought Severity Index (PDSI) data for July and August. PDSI integrates precipitation and moisture into a single variable as a representation of drought conditions (Palmer 1965; Guttman 1991). Positive values of PDSI indicate wetter and cooler than normal conditions while negative values indicate drier and warmer conditions than normal. Daily maximum and minimum temperature data were also obtained for Hamilton, MT to identify short-term cold snaps that may be related to reductions in forest area killed.

Results and Discussion

Dendrochronology

Death dates were determined for 84 of 110 (76%) sampled whitebark pines (Table 1). Eroded outer rings, poor crossdating characteristics (too few annual growth rings or complacent growth), and suppressed growth limited the determination of death dates of 26 sampled trees. Whitebark pine mortality due to mountain pine beetle epidemics is clustered around a few short time periods, with the largest peak centered around 1930 (Figure 3). Mortality events also occurred in 1960s, and 1980s (Figure 3, Table 1). These events during the 1960s and 1980s were restricted to the Beaver Lake and Burnt Knob Lake Basins respectively (Table 1). The 1930s outbreak is evident elsewhere in the Northern Rocky Mountain Region according to historical documents (e.g., Evenden 1944), and dendrochronological evidence (Perkins and Swetnam 1996). Four trees also suggested mortality due to mountain pine beetle occurring during the 1870s, however, outer rings were too decayed to ensure accurate assignment of annual dates (data not shown).

Dendrochronology is a useful tool for the identification or verification of past mountain pine beetle epidemics. The existence of large numbers of beetle killed whitebark pine snags in the three watersheds examined were expected to provide the

dates of multiple beetle epidemics through time. Unfortunately, we could not reliably identify beetle-induced tree mortality prior to the 20th century as we had hoped. Our results suggest most of the mortality we observed was the result of one, region-wide outbreak that peaked around the late 1920s and early 1930s. This region-wide outbreak is well documented by written accounts (Evenden 1944) as well as dendrochronological evidence from the Salmon-Sawtooth area of central Idaho (Perkins and Swetnam 1996). Evenden (1934) suggests a mountain pine beetle outbreak beginning in 1909 in the Flathead National Forest spread southward to the Bitterroot National Forest reaching epidemic proportions by 1924. Tree mortality, largely occurring in lodgepole pine, was evident during most years of the outbreak, but a relatively quiet period between 1913-1924 was also noted (Evenden 1944).

Dendrochronological evidence corroborates the temporal patterns of mortality noted by historical accounts. Mortality in whitebark pine forests was present but low during the early 1920s before increasing dramatically from 1927 to 1931 (Figure 3). The epidemic in whitebark pine in the SBW apparently began to subside between 1931 and 1934. Evenden (1934) indicates the mountain pine beetle epidemic being monitored in the Beaverhead National Forest subsided substantially during 1933 as a result of high mortality of over wintering bark beetle broods due to a period of cold weather in the vicinity.

Temperature and precipitation patterns during the 1930s outbreak may help to explain the onset of widespread beetle-induced tree mortality in the SBW. Summer temperatures were generally warm throughout the 1920's, although summer precipitation was not anomalously low (compare Figure 3A and 3B). The dramatic increase in beetle-induced tree mortality around 1928 and 1929 appears to have coincided with temperature and moisture conditions adverse for tree growth. Summer PDSI decreased dramatically from the late 1910s and lasted through much of the 1930s indicating drought conditions. Drought conditions may have predisposed otherwise healthy trees to successful colonization due to compromised defenses resulting from moisture stress, but at relatively low levels. Beetle populations may have grown steadily throughout the drought period eventually reaching epidemic proportions after the drought's initial onset (Berryman 1976). It is plausible that whitebark pines did not

experience extreme moisture stress until both temperature and precipitation became extreme. Warm summer temperatures are generally favorable for whitebark pine growth so long as moisture is not limiting (K.F. Kipfmueller, in prep.). Interestingly, trees with death dates earlier in the outbreak period also had been scarred by fire, while those exhibiting death dates near the end of the period had no apparent injuries. Fire-scarred trees may have served as infection centers providing beetles to infect uninjured or otherwise healthy trees when widespread drought conditions materialized later in the epidemic. Interestingly, the driest summer of the outbreak occurred in 1931, a period when mortality appears to be declining. This apparent decline may be due to a limited number of living whitebark pine available for beetles to colonize, making it appear as if a decline in the outbreak was occurring when actually mortality may have already depleted the available food resource earlier in the epidemic. On the other hand, winter brood mortality may have reduced the population of beetles to a level below which successful attacks were possible (see discussion below).

A decrease in beetle-induced tree mortality is evident during 1930 in the sampled whitebark pine (Figure 3). This reduction during the summer of 1930 may be due in part to a dramatic cold snap during the previous winter that may have led to considerable bark beetle brood mortality. Maximum daily temperature recorded at Hamilton, MT between January 13 and January 24, 1930 averaged only -17 C, with a maximum temperature of only -13 C (Table 2). Minimum temperatures for the same time period averaged -31C with highest recorded minimum temperature of -24 C (Table 2). This cold snap would likely have been of sufficient duration to induce mortality, particularly since most of the beetle populations were occupying elevations approximately 1,350 m higher than those of the Hamilton climate station and likely experienced much lower temperatures. Evenden (1936) found beetle mortality to be high during a January cold snap in 1935 with reduced beetle activity during the following summer (Table 2). While the temperature patterns presented by Evenden are generally cooler, the cold snap of 1930 near Hamilton is of longer duration. It seems possible that bark beetle mortality patterns in 1930 in the SBW were similar to those found by Evenden (1936) following the 1935 cold snap. The apparent cessation of the outbreak during the early 1930s is likely due to similar winter temperature patterns occurring during February 1933 that

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resulted in reduced beetle activity reported for the Beaverhead National Forest located nearby the SBW (Evenden 1934).

Aerial Survey Data

Two region-wide mountain pine beetle outbreaks have occurred since about 1966 (Figure 4). The first outbreak began gradually around the late 1970s and peaked during the mid 1980s (Figure 4). A second epidemic started around 1994 but does not appear to have yet peaked (Figure 4). There are, however, several dramatic reductions in area affected during the course of the outbreaks. For example, area affected was generally high during most of the 1980s, but decreased dramatically during 1984.

Like fluctuations in tree mortality identified during the 1930's outbreak, these fluctuations in beetle activity could also be related to the patterns of winter and summer temperature in the region. Temperatures during July of 1975 are warmer than the long-term summer average and temperatures during the following winter (1976) appear to be somewhat warmer than normal (Figure 5a). In addition, 1977 is generally warmer throughout the year than the long-term average (Figure 5a). The increasing beetle activity around this time may be related to favorable climatic conditions leading to increased brood production and survival during the summer and through the winter months (compare Figures 4 and 5). While temperatures were not extremely high during July 1977, the observed short period of warm temperatures over the region may have aided in the synchronization of life cycles and emergence of adult beetles leading to effective mass attack (Logan et al. 1998). Temperatures were again mild through the winter of 1980/1981 and average August temperature was slightly above average during 1981 (Figure 5b). The increase in beetle activity during 1981 could be related to this pattern of mild winters and warmer summers. Mild winters limit over wintering mortality and relatively warm periods during the summer synchronize emergence leading to successful mass attacks.

The level of beetle activity detected by aerial surveys decreased in 1984 from those of the previous year (Figure 4). This reduction in activity may be related to cold snaps that occurred during December 1983 and January 1984 (Figure 5b). Average maximum temperature recorded at Hamilton between December 18-25 was -18.0 C

(range -23 to -13). Minimum daily temperature over the same period averaged only -26.7 C (range -34 to -16). Winter temperatures were again cooler than average during the winters of 1985 and 1986 and may have inhibited beetle activity during subsequent summers, resulting in an overall decrease in mountain pine beetle activity through the late 1980s (compare Figures 4 and 5b). Similar temperature patterns exist in the middle 1990s surrounding the most recent mountain pine beetle outbreak, but winter temperatures were consistently warmer than the long term average throughout the period (Figure 5c).

Lodgepole pine forests appear to be the most common host species in the Selway-Bitterroot region (Table 3). Almost a quarter million ha (249,882) in lodgepole pine forests between 1966-1998 were identified as having experienced beetle-induced tree mortality. Considerably less area experienced mortality in ponderosa pine (35,249 ha) and whitebark pine (6,145 ha) during the same period. These differences are probably at least partly explained by the differences in area occupied by these cover types. Lodgepole pine forests are likely the most common of the three habitat types followed by ponderosa and whitebark pine.

While the proportionally high beetle-induced tree mortality in lodgepole pine is most likely due to the disproportionate amount of lodgepole pine forests with respect to other potential host species in the area, there may be at least one other potential explanation for the large amounts of lodgepole pine mortality between 1966-1998. It is possible that lodgepole pine forests in the region are now increasingly susceptible to mountain pine beetle epidemics because they are beginning to reach maturity over a large area (Schmidt 1989; Hagle and Schmitz 1993). Region-wide fires during the late 19th and early 20th centuries resulted in the regeneration of large areas (Rollins et al. 2001); many now support lodgepole pine forest with tree diameters preferred by the mountain pine beetle. The diameter of lodgepole pines in 10 stands burning ≈100 years ago averaged 18 cm (Kipfmueller unpubl. Data). Amman and Safranyik (1985) suggested lodgepole pine stands of around 80 years in age with average diameters approaching 20 cm are at high risk of beetle epidemics. Lodgepole pine forests that are beginning to reach maturity may be at higher risk across these large areas than earlier in the century.

Several authors suggest mountain pine beetle epidemics begin in lower elevation forests before moving upwards into higher elevation forests (e.g., Baker et al. 1971; Parker 1973; Amman and McGregor 1985; Arno and Hoff 1990; Bartos and Gibson 1990). Aerial survey data for the three national Forests examined in this study weakly support a limited spatial relationship between beetle epidemics and migration to higher elevations. Beetle mortality appears to peak around the middle 1970s in ponderosa pine hosts in both the Bitterroot and Lolo National Forests before peaking around 1982-83 in lodgepole pine hosts (Figure 6). The relationship with whitebark pine, however, is not as clear, primarily because only a limited area is affected within whitebark pine communities (Figure 6).

Bartos and Gibson (1990) suggest that mountain pine beetles in northern Idaho and western Montana prefer lodgepole pine over ponderosa pine, followed by whitebark pine. This preference may result in epidemics spreading not simply from lower elevations to higher elevations, but might result in epidemics beginning in lodgepole pine forests and spreading both upward and downward in elevation during epidemic years. The aerial survey data used here is too coarse to examine these relationships in greater detail. However, this relationship could have important effects on the propagation of mountain pine beetle epidemics across a region.

Aerial Survey Data and Climate Connections

Pearson correlations between the beetle mortality data from the three National Forests and Idaho Climate Division 4 data for different temperature and precipitation data indicate the strongest relationship between beetle-induced tree mortality (total hectares killed) and climate relates to July precipitation (Table 4). When individual host species are considered individually, lodgepole pine, whitebark pine, and a subalpine category consisting of these two cover types combined, are all significantly correlated with July precipitation amounts ($P \leq 0.001$). Whitebark pine also has a significant, but slightly lower correlation with July-August PDSI ($P \leq 0.05$). No significant correlation exists between area affected and the climate variables considered for ponderosa pine when individual host species are considered ($P \geq 0.05$).

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Regression models to predict hectares affected from July precipitation were constructed for square root transformed total area, lodgepole pine, whitebark pine and the subalpine cover type variables. Variance explained ranged between 22% and 24% for all four regression models (Table 5). Model 1, which uses total area affected and July precipitation, was the only model with both the slope and intercept significant (Table 5). An additional regression model was constructed using July precipitation and prior year mortality to estimate current year mortality (total hectares killed). This model explained approximately 73% of the variance in current year mortality, but parameter estimates for July precipitation were no longer significant ($P \geq 0.05$).

Positive relationships between moisture balance and insect epidemics have been identified in a number of studies relating insect epidemics to climate (e.g., Swetnam and Lynch 1993; Logan et al. 1998). In the case of the mountain pine beetle, above average July precipitation may actually serve to reduce a host tree's capacity to resist beetle attacks, thereby resulting in an increase in colonization and subsequent mortality. Wetter summers might create optimum conditions for tree-growth, expressed as radial expansion, while at the same time limiting the production of defensive compounds, following the hypothesis put forth by Lorio (1986) and Lorio and Sommers (1986).

The somewhat contradictory relationships between the dry period surrounding the mountain pine beetle outbreak in the 1930s and the positive relationship between July precipitation and mountain pine beetle outbreaks between 1966 to1998 seem to support Lorio's (1986) and Lorio and Sommers (1986) conceptual frameworks. The 1930s outbreak, for example, may be primarily due to extreme water stress that reduced the capacity of host species to resist mountain pine beetle attacks. Moisture stress may have provided a suitable, and easily exploited food source across a large area resulting in a widespread epidemic. However, beetle activity between 1966 to1998 may be more closely related to favorable growing conditions that resulted in a shift in host trees' resources away from the production of defensive compounds and toward the allocation of energy and photosynthate to growth processes. These later epidemics (1966-1998) may then be related to a reduction in tree resistance, not necessarily through water stress, but rather due to shifts in the host species allocation of energy and food. These potential nonlinear relationships between climate and mountain pine

beetle epidemics complicate attempts at linking mountain pine beetle activity to climate and suggest there may be multiple climatic conditions that predispose forests to outbreaks of mountain pine beetle.

The regression model that included mortality from the previous year (model 5) explains a large amount of variance, yet July precipitation was no longer significant in the regression equation. Partial autocorrelation of the total hectares killed by mountain pine beetles is quite high and positive at a one-year lag (Figure 7). The population level of mountain pine beetle during the previous year appears to impart more power in the regression than does July precipitation. This suggests that while July precipitation is an important feature of mountain pine beetle epidemics, it may not have much to do with the level of mortality per se, but instead may enable already high populations of beetles to overcome hosts that are not stressed by other environmental factors such as drought, and eventually reach epidemic population levels. Mortality is likely to be high due to an abundance of beetles capable of aggregating on trees, particularly when conditions are also favorable for tree-growth.

While it is tempting to link broad-scale mountain pine beetle epidemics with broad-scale climatic patterns, the process is hampered by the complex interactions among the beetles and their hosts. Epidemics may begin building in individual trees that may be injured by lightning or fire. This small, dispersed population may maintain itself under endemic conditions by colonizing other individual trees throughout a stand resulting in scattered "salt and pepper" mortality. Abiotic conditions, such as a short period of drought, may eventually occur that "releases" the endemic population resulting in a rapid buildup of beetles. When growing conditions return to near normal the beetle population may be sufficiently large to be able to overwhelm even vigorously growing trees, prolonging the outbreak (Berryman 1976). Trees growing under optimal conditions may provide an ideal food source resulting in continued population build-ups and a positive feedback loop. The beetle epidemic will then likely continue until some other factor results in high beetle mortality. Beetle mortality could result either through a reduction in available food supply (the epidemic runs its course) or a short-term weather anomaly such as a winter cold snap leading to failed or reduced reproductive success.

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In any case it seems reasonable that beetle-induced tree mortality could be related to either favorable growing conditions for the host or conditions that result in stress.

Implications for Whitebark Pine Management

Mountain pine beetle epidemics in whitebark pine are apparently rare in comparison to lodgepole pine or ponderosa pine forests (Bartos and Gibson 1990). Climatic conditions in whitebark pine habitats may be too cold to consistently produce the high populations of mountain pine beetles necessary to propagate periodic epidemics. Mountain pine beetles in whitebark pine forests often require two years to complete their life cycle reducing the probability that populations within these forests will reach epidemic proportions (Amman and McGregor 1985). Further, cool temperatures at upper elevations have been shown to reduce host mortality due to the long developmental periods required to complete a single generation (Amman et al. 1977). Cool temperatures may result in delayed emergence of adults and therefore delayed construction of galleries and egg laying leading to a higher proportion of winter mortality in upper elevation stands.

Whitebark pine mortality due to mountain pine beetles may be relatively infrequent occurring only during periods when beetle populations are at epidemic proportions at lower elevations, or only when drought is prolonged. Even if these events are infrequent, the losses are significant, especially given the ecological importance of the species and its current documented decline (Tomback et al. 2001). Increases in shade tolerant species such as subalpine fir and Engelmann spruce within whitebark pine communities due to fire suppression may have the effect of increasing the potential for future beetle epidemics by altering competitive relationships (Morgan and Bunting 1990; Keane and Arno 1993; Murray et al. 1998). Whitebark pine resistance to beetle attacks may be further compromised by the invasion of white pine blister rust leading to a reduced capacity of whitebark pine to resist beetle attacks (Keane and Arno 1993; Tomback et al. 1995; Campbell and Antos 2000). The whitebark pine mortality documented using dendrochronological techniques and attributed to the mountain pine beetle coincides with the first widespread mortality due to blister rust in the northern Rockies (see Figure 10-2 in McDonald and Hoff 2001). It

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is possible that blister rust infection accelerated or extended the size and severity of mountain pine beetle-induced tree mortality and predisposed whitebark pine trees to successful attack by beetles around the 1930s outbreak.

It is widely believed global temperatures are rising due to increasing concentrations of greenhouse gasses (Mann et al. 1998; IPCC 2001). Species existing at the margin of their ecological limits, such as subalpine conifers, are expected to be among the most heavily impacted by shifts in climate (Bartlein et al. 1997; Shugart 1998). Although mountain pine beetles currently appear to require two years to complete their life cycle in whitebark pine forests, it is plausible that rising temperatures could result in an increase in growing season length and might serve to reduce the time necessary for mountain pine beetles to complete their life cycle in these forests. Further, an increased frequency of warm dry conditions could result in an increase in conditions that result in moisture stress in whitebark pines. These factors may all serve to increase the probability of future epidemics of mountain pine beetle in whitebark pine forests and hasten the species already rapid decline in the region.

An understanding of the ecology of the mountain pine beetle with respect to whitebark pine is necessary to manage whitebark communities for sustainability in the face of climate change and the effects of blister rust. Currently, most research concerning the role of mountain pine beetle in forests of the northern Rocky Mountains has focused on commercially important species such as lodgepole and ponderosa pine. While this research is clearly informative, whitebark pine-beetle interactions may be different and further research in these species interactions is needed.

Conclusions

Dendrochronological techniques have been used successfully to reconstruct large scale patterns of insect outbreaks in a number of areas (Swetnam and Lynch 1993; Swetnam et al. 1995; Perkins and Swetnam 1996; Ryerson 1999; Speer 2000). In this study dendrochronological techniques corroborated evidence of an earlier mountain pine beetle epidemic in whitebark pine forests that occurred around 1930. In this region, however, it is difficult to identify older outbreaks because periodic fires consume much of the evidence, or decay processes limit the interpretation of mortality

events to the relatively recent past. Outer rings that are necessary to substantiate mortality are often eroded preventing the assignment of exact calendar dates of death and precluding comparisons with climate.

Both abnormally cool and warm temperatures appear to be related to mountain pine beetle epidemics in the Selway-Bitterroot region. Warm temperatures may have both direct and indirect effects on mountain pine beetle populations. Direct effects include increasing the probability of survival of over wintering broods that can attack large numbers of hosts the following year. Indirectly, warm temperatures may act in concert with reduced precipitation to reduce hosts' capacity to repel mountain pine beetle attacks. Cold temperatures, particularly during the winter months may result in significant over-wintering mortality of mountain pine beetle broods resulting in a temporary reduction in beetle activity during the subsequent summer.

There appear to be two possible pathways linking climate and mountain pine beetle epidemics. Drought conditions, such as those occurring around the 1930s outbreak, may result in widespread moisture stress limiting the production of defensive compounds in hosts necessary to repel colonizing beetles. However, positive relationships between July precipitation and beetle-induced tree mortality may also limit a host's capacity to produce defensive compounds by altering growth-differentiation relationships within hosts (Lorio 1986; Lorio and Sommers 1986).

The effective suppression of fires in the region throughout most of the 20th century (Rollins et al. 2001) has led to homogenous forests at risk to beetle epidemics. Mature lodgepole pine forests capable of supporting large mountain pine beetle populations now likely occupy large areas that burned around the turn of the century. In addition, increased competition from shade tolerant species within these forests may impart stress due to increased competition for resources providing opportunities for endemic populations of beetles to grow and expand as environmental conditions change periodically. A large scale drought, for example, may result in region wide moisture stress that could trigger mountain pine beetle epidemics in these contiguous forests.

Dendrochronology has not been extensively used in the examination of mountain pine beetle epidemics but can be applied to answer important questions regarding

beetle ecology. While dendrochronological techniques can be applied toward understanding broad-scale beetle-climate relationships, it can just as easily be used to address micro-scale interactions. For example, the spatial progression of a mountain pine beetle epidemic within a stand could be investigated by determining death dates from trees successively killed by bark beetles. This would aid in the identification of past infection centers as well as the spatial propagation of an epidemic. Coupled with ring-width measurements, the onset of moisture stress or other growth relationships could be examined that may help identify important lagging relationships between the factors that lead to build ups in the beetle population and the onset of epidemic infections.

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Table 1. Location and characteristics of three watersheds sampled for dendrochronological analysis of mountain pine beetle-induced mortality.

Watershed Name	Location (Lat./Lon.)	Elevation (m)	No. of Trees Sampled	No. of Trees Dated (%)	Mortality Events
Burnt Knob Lake	45.7°N, 115.0°W	2,500	37	26 (70)	1930's, 1980's
Beaver Lake	46.6°N, 114.4°W	2,250	29	22 (75)	1930's, 1960's
Baker Lake	45.9°N, 114.2°W	2,670	44	36 (81)	1930's

Table 2. Comparison of daily maximum and minimum temperatures (°C) for the cold snap of 1930 in Hamilton, MT to 1935 cold snap data presented in Evenden 1936.

Hamilton, Montana			Hutchins, Montana			Virginia City, Montana		
Date	Max T (°C)	Min T (°C)	Date	Max T (°C)	Min T (°C)	Date	Max T (°C)	Min T (°C)
1/13/30	-13	-26	1/17/35	-2	-23	1/17/35	-8	-12
1/14/30	-13	-27	1/18/35	-23	-28	1/18/35	-21	-23
1/15/30	-16	-26	1/19/35	-28	-34	1/19/35	-30	-32
1/16/30	-17	-24	1/20/35	-26	-38	1/20/35	-34	-34
1/17/30	-22	-36	1/21/35	-5	-26	1/21/35	-12	-26
1/18/30	-21	-34	Average	-17	-30	Average	-21	-26
1/19/30	-16	-28						
1/20/30	-16	-33						
1/21/30	-18	-35						
1/22/30	-18	-34						
1/23/30	-16	-33						
1/24/30	-14	-33						
Average	-17	-31						

Table 3. Mortality recorded by aerial survey data for three National Forests near the Selway-Bitterroot Wilderness Area between 1966-1998. Area (hectares) is stratified by host species.

	Ponderosa Pine	Lodgepole Pine	Whitebark Pine
Total Area (1966-1998)	35,249	249,883	6,145
Mean Annual Area	1,068	73,159	186

Table 4. Correlations between climate variables and aerial survey mortality data, 1966-1998. Climate variables are from Idaho Climate Division 4 (T=temperature, P=precipitation). Asterisks represent the significance of the Pearson correlation coefficient (*$P \leq 0.05$, **$P \leq 0.01$).

Climate Variable	Mortality Variable (Square root transformed)				
	Total	PIPO	PICO	PIAL	SUBALP
DEC T (prior year)	0.013	-0.095	-0.033	0.249	-0.024
JAN T	0.016	-0.168	-0.050	0.192	-0.042
FEB T	-0.186	0.012	-0.138	-0.198	-0.140
MAR T	0.289	0.192	0.394	0.243	0.394
JUN T	0.069	0.236	0.108	-0.072	0.104
JUL T	-0.139	-0.077	-0.139	-0.108	-0.139
AUG T	0.094	-0.039	-0.016	0.075	-0.012
JUN P	-0.065	-0.220	-0.145	-0.004	-0.141
JUL P	0.500**	0.250	0.498**	0.493**	0.503**
AUG P	-0.024	-0.137	0.005	0.116	0.008
July-Aug PDSI	0.254	-0.054	0.198	0.407*	0.206

Table 5. Regression models developed using aerial survey data and July precipitation. Mortality variables were square root transformed prior to regression analysis.

Model 1: Total Area

Parameter	Coefficient	S.E.	t-value	P (two tail)	Adjusted R^2	F-Ratio
Constant	42.16	14.24	2.96	0.006	0.235	10.84
July Precip	15.61	4.74	3.29	0.002		

Model 2: Lodgepole Pine Hosts

Parameter	Coefficient	S.E.	t-value	P (two tail)	Adjusted R^2	F-Ratio
Constant	28.11	15.79	1.78	0.085	0.224	10.21
July Precip	16.81	5.26	3.20	0.003		

Model 3: Whitebark Pine Hosts

Parameter	Coefficient	S.E.	t-value	P (two tail)	Adjusted R^2	F-Ratio
Constant	-1.40	3.54	-0.40	0.695	0.219	9.96
July Precip	3.718	1.18	3.16	0.004		

Model 4: Subalpine Category

Parameter	Coefficient	S.E.	t-value	P (two tail)	Adjusted R^2	F-Ratio
Constant	27.67	15.98	1.73	0.093	0.229	10.53
July Precip	17.27	5.32	3.25	0.003		

Model 5: Total Area and Lagged Mortality

Parameter	Coefficient	S.E.	t-value	P (two tail)	Adjusted R^2	F-Ratio
Constant	8.07	9.92	0.81	0.423	0.751	43.74
July Precip	3.94	3.12	1.26	0.217		
Prior Year Mortality	0.83	0.11	7.86	0.000		

Figure Headings

Figure 1 (Front Cover). "Ghost forest" of whitebark pine snags killed by mountain pine beetles during the late 1920s-1930s outbreak near Beaver Lake, Idaho in the Selway-Bitterroot Wilderness Area (Photo by K.F. Kipfmueller, 1998).

Figure 2. Study site locations of dendrochronologically determined whitebark pine mortality dates within the Selway-Bitterroot Wilderness Area, in Idaho and Montana. Sample sites are indicated by white triangles. Heavy dark line represents the boundary of the wilderness area. Darker colors indicate areas or lower elevations while lighter colors indicate higher elevations. Inset maps show the locations on the Idaho/Montana border of the Selway-Bitterroot Wilderness Area and the four National Forests with administrative responsibilities.

Figure 3. Whitebark pine mortality identified using dendrochronological dating techniques for three sampled watersheds. Black bars=Burnt Knob Lake, Gray=Beaver Lake, White=Baker Lake. (A) July-August total precipitation (cm). (B) Average July-August temperature (°C). (C) Average July-August Palmer Drought Severity Index (PDSI). All climate data is for Idaho Division 4 obtained from the National Climatic Data Center (NCDC). Dotted lines indicate the longterm mean of each climate series (1900-2000).

Figure 4. The percentage of forest area killed by mountain pine beetle 1966-1998 as mapped by aerial surveys. (A) Percentage of mortality in three individual National Forests. (B) Percentage of mortality in three National Forests combined.

Figure 5. Idaho Climate Division 4 annual temperature patterns for various years expressed as standard deviation units based on 1900-2000 time period. (A) Annual temperature patterns from 1975 to 1977, (B) annual temperature patterns from 1980 to 1987, (C) annual temperature patterns 1994-1998.

Figure 6. The percentage of forest area killed by mountain pine beetles identified using
aerial survey mapped beetle mortality from 1966 to 1998 for three National Forests by
host species. Note that the scale of the Y-axis on the three graphs differs.

Figure 7. Partial autocorrelation of total area of mountain pine beetle-induced tree
mortality across all three National Forests. The dotted line indicates the approximate
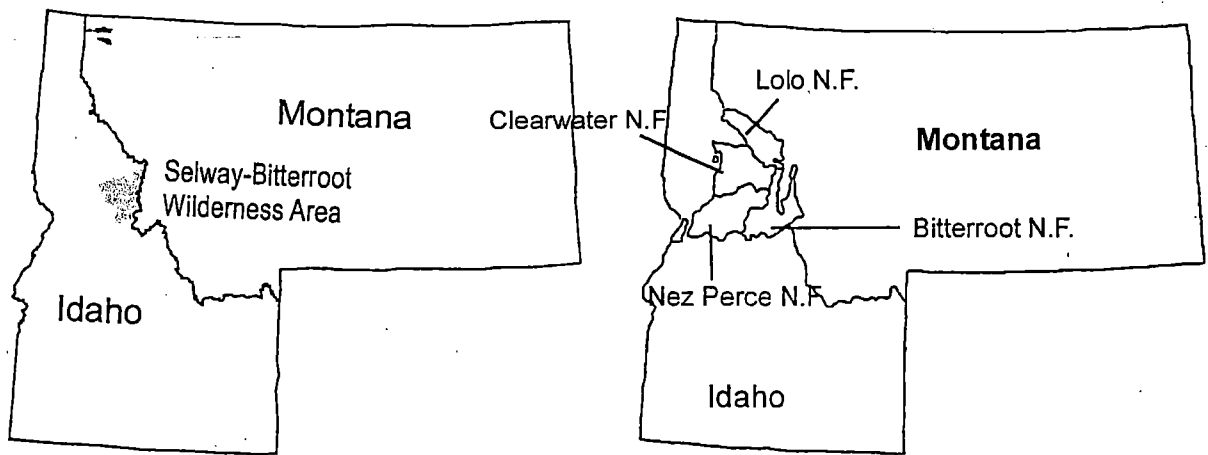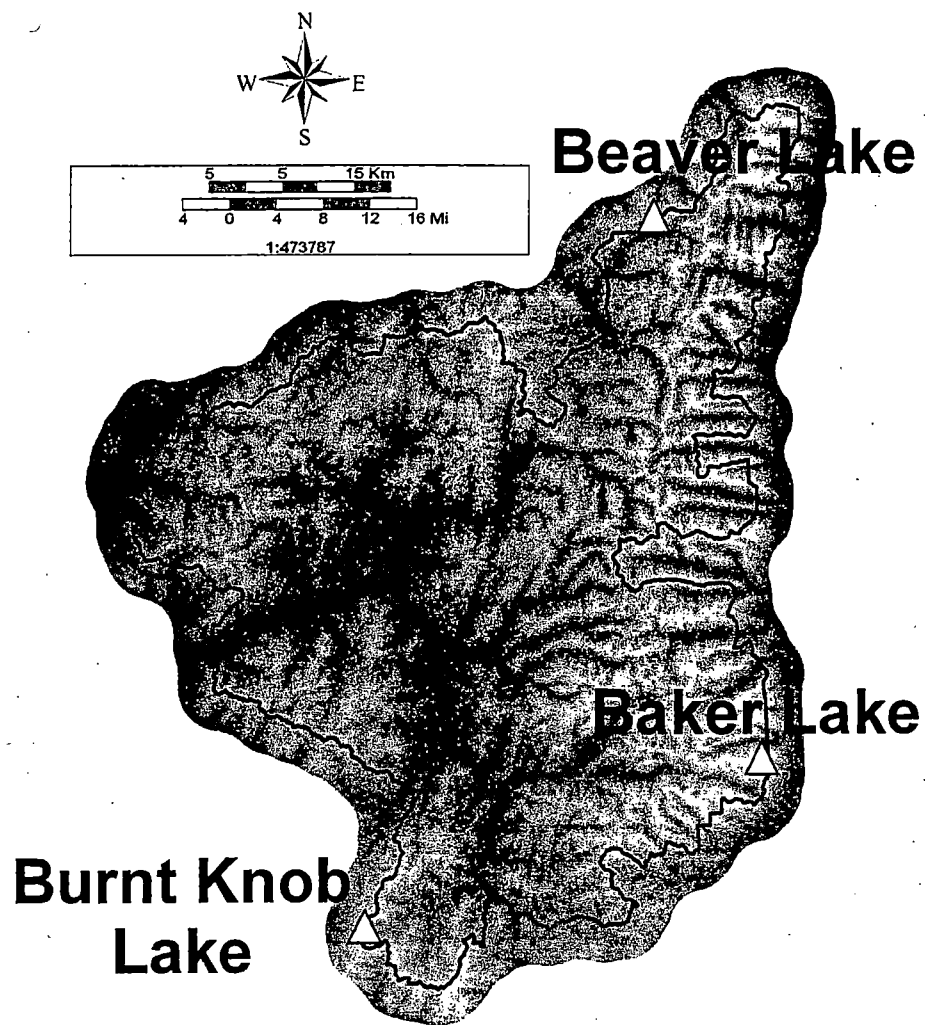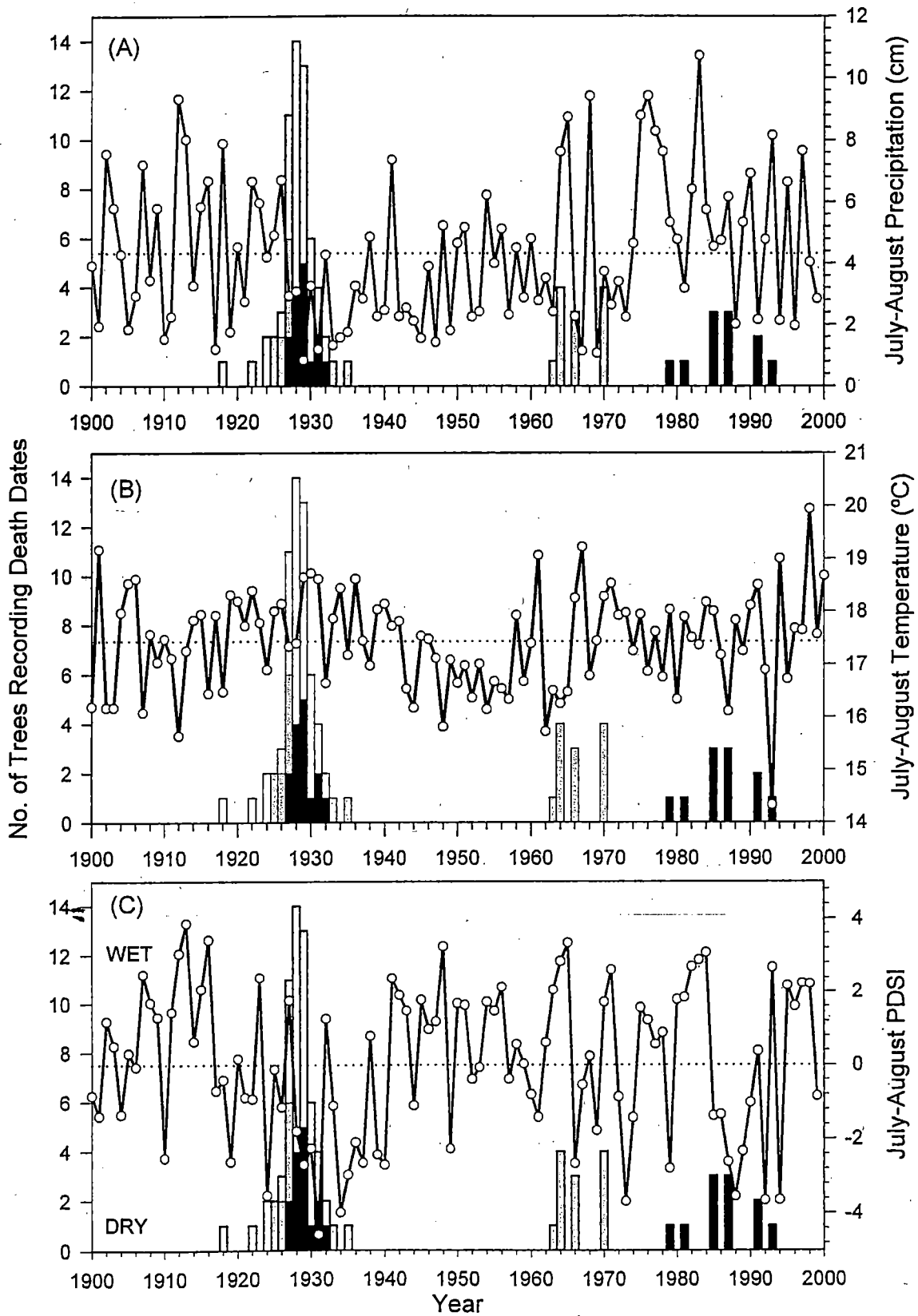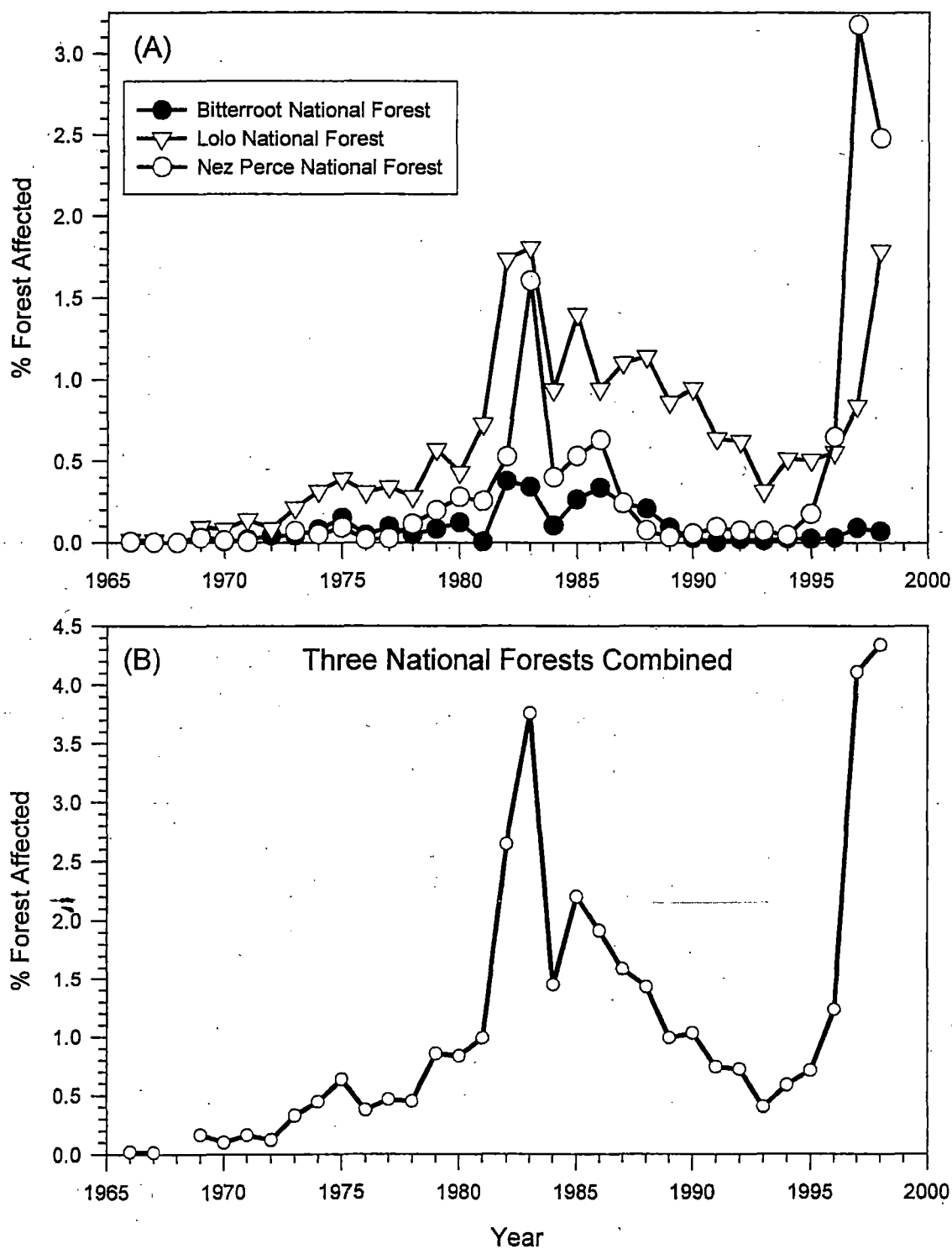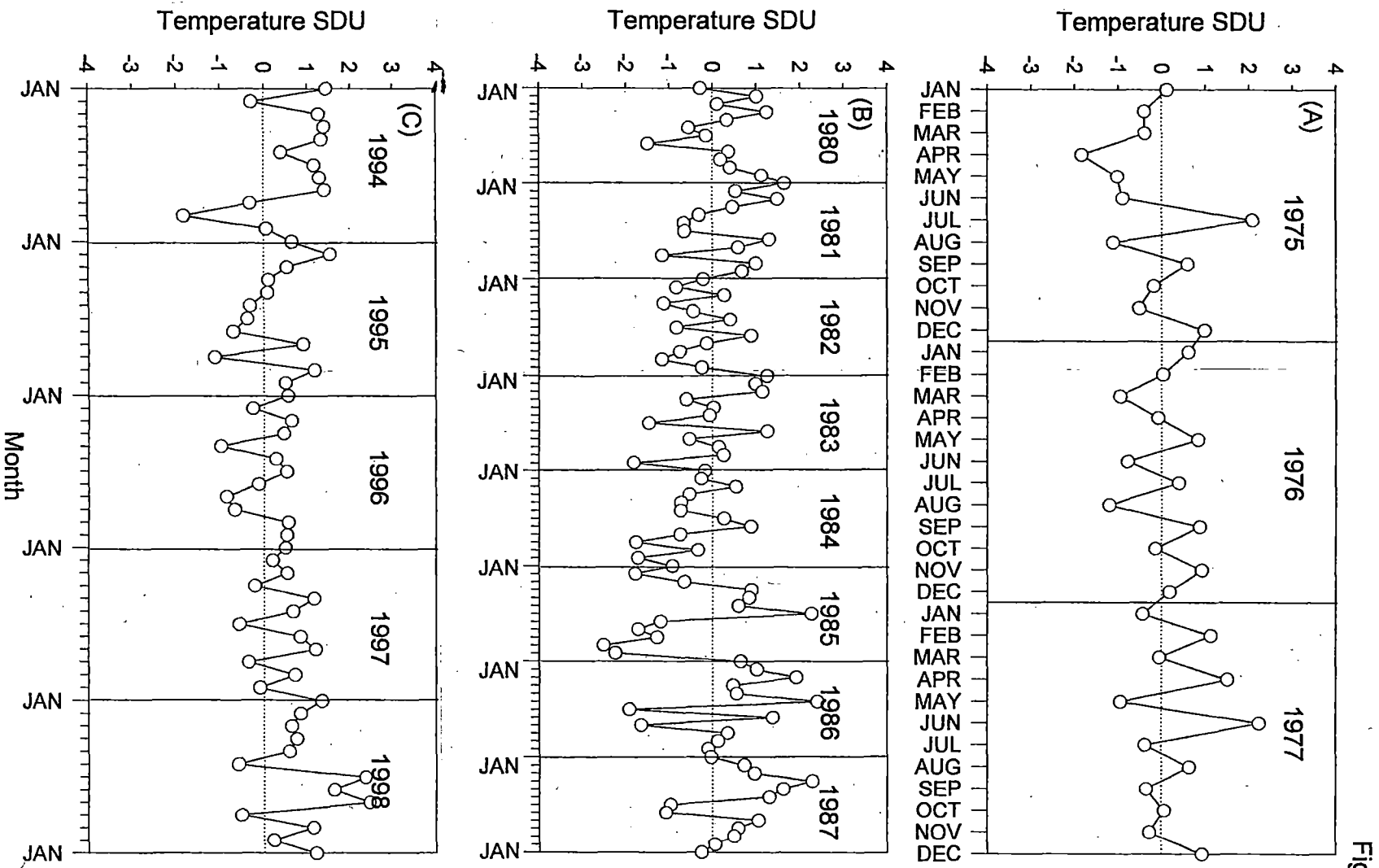95% confidence limits.

Figure 2

Figure 3

Figure 4

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Figure 5

Figure 6

Figure 7